PROC. ENTOMOL. SOC. WASH.
104(4), 2002, pp. 1007–1028

THE FAUNA OF TEPHRITIDAE (DIPTERA) FROM CAPITULA OF ASTERACEAE IN BRAZIL

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Abstract.—This is the first comprehensive survey of the fauna of Tephritidae that breed in capitula of Asteraceae in southern and southeastern Brazil, resulting from a sampling program begun in 1985. The Tephritidae is the most diverse and abundant family of endophages of Asteraceae flowerheads in Brazil. From approximately 1,800 samples of capitula from 403 species of Asteraceae, we reared 9,697 Tephritidae individuals belonging to 80 species and 18 genera. Of these, at least 31 species and 3 genera are undescribed, and 30% of the described species were not previously recorded from Brazil. The most diverse tribes of Asteraceae in the Neotropics, Vernonieae and Eupatorieae, have the greatest diversity of associated tephritids, although Vernonieae has a greater number of specialist species. Although the tribe Senecioneae is moderately diversified in the studied area, it is rarely attacked and has no specialist tephritid species, in contrast with other areas of the world. The tephritid fauna in Brazilian Asteraceae flowerheads is dominated by Neotropical genera (e.g., *Tomoplagia*, *Xanthaciura*, *Dictyotrypeta*, *Tetreuaresta*, and *Trypanaresta*) that represent 80% of the obtained species and 90% of the obtained individuals. Most of these tephritid species are restricted to one tribe or some lower taxonomic level of Asteraceae. The main host plants for 75% of them belong to one genus or group of related genera of host plants. Most of our host records for genera and species of tephritids agree with previously published records from other world regions, showing that there is little variation in the set of host plants of tephritid species and genera among areas. The geographic distribution and host plants for each genus are discussed, and a list of host plants and localities is presented, for the identified species, totaling 167 new host records.

Key Words: Tephritidae, Asteraceae, host records, checklist

Tephritidae are well known mainly because of the economic importance of various species of the subfamilies Trypetinae and Dacinae, whose larvae are pests of fleshy fruits (e.g., many species of the genera *Anastrepha*, *Dacus*, *Bactrocera*, *Rhagoletis* and *Ceratitis*). However, Asteraceae is the most important host family for Te-

phritidae worldwide (Zwölfer 1988, White and Elson-Harris 1992, Foote et al. 1993). The larvae of most species of the large subfamily Tephritinae breed in Asteraceae, forming galls in various parts or feeding in capitula, and some Trypetini (Trypetinae) mine stems or leaves of Asteraceae (Foote et al. 1993, Norrbom et al. 1999a, Han 1999). The association with Asteraceae is ancient and seems to have been a major factor in tephritid diversification (Zwölfer 1988, Straw 1989a, b). The high diversity and cosmopolitan distribution of the Tephritinae suggest the occurrence of a great radiation after the colonization of Asteraceae. Knowledge of Neotropical Tephritidae is still very incomplete, and is more developed for groups with economic relevance, mainly the genus *Anastrepha*. There is little information on the biology of most species, especially the Tephritinae, and even their taxonomy is far from complete (Foote 1980, Foote et al. 1993).

In Brazil, we started an extensive survey of endophagous insects of Asteraceae in 1985 to investigate the factors determining the local and regional richness in phytophagous insect communities (Lewinsohn 1988, 1991). The capitula of Asteraceae concentrate food in a protected place, and, as a result, shelter a rich and diversified fauna of endophagous insects (Zwölfer 1979, 1982, 1988; Lewinsohn 1988, 1991). Females of these insects lay their eggs on or in the capitula, and the larvae develop inside them, eating sap, flowers, ovules and/or fruits (Zwölfer 1979, 1988; Straw 1989a, b; Gielis 1993; Gagné 1994; Almeida 1997). In southern and southeastern Brazil, the main endophages of Asteraceae capitula belong to three Diptera families (Tephritidae, Cecidomyiidae and Agromyzidae) and four Lepidoptera families (Tortricidae, Pterophoridae, Pyralidae, and Gelechiidae), totaling at least 117 species (Lewinsohn 1988, 1991; Lewinsohn and Prado, in press; Lewinsohn et al., unpublished data). In temperate regions, the Tephritidae are always one of the families with greatest species richness and abundance among flower-head feeders (Zwölfer 1982, 1988; Sobhian and Zwölfer 1985, Straw 1989b; Foote et al. 1993).

The organization patterns of endophagous guilds in Brazilian Asteraceae flowerheads have already been partially analyzed (Lewinsohn 1991, Prado and Lewinsohn 1994, 2000), but a complete list of the species and genera that comprise these guilds has not yet been published. Here, we present the compiled records of Tephritidae reared from Asteraceae capitula sampled through 13 years at 48 localities in southern and southeastern Brazil. We characterized this insect fauna according to its composition, distribution and host plant use. We also present lists of the sample localities, and of the host plants of the described species.

Methods

The data presented in this study were obtained from surveys of endophagous insects in Asteraceae flowerheads we made in southern and southeastern Brazil from 1985 to 1998. The majority of the data are from two surveys: from 1985 to 1988, seventy species of Asteraceae representing the main habitats, extent of geographical distribution, and taxonomic groups were sampled in eight areas of southeastern Brazil (Lewinsohn 1988); and from 1995 to 1997, we carried out a broader survey, expanding sampling for all Asteraceae to 32 localities within the states of Minas Gerais, Santa Catarina and Rio Grande do Sul. Apart from these extensive surveys that included the whole endophagous fauna, we also included data from more restricted samples, including: a one-year intensive survey of tephritids on plants of the tribe Vernonieae in Serra do Cipó (data for the genus *Tomoplagia* were partially compiled by Prado and Lewinsohn, 1994, but are updated here); surveys of capitula endophages of *Praxelis clematidea* (Griseb.) R. King and H. Rob. (Ortiz 1997) and *Trichogoniopsis adenantha* (DC.) R. King and H. Rob. (Almeida

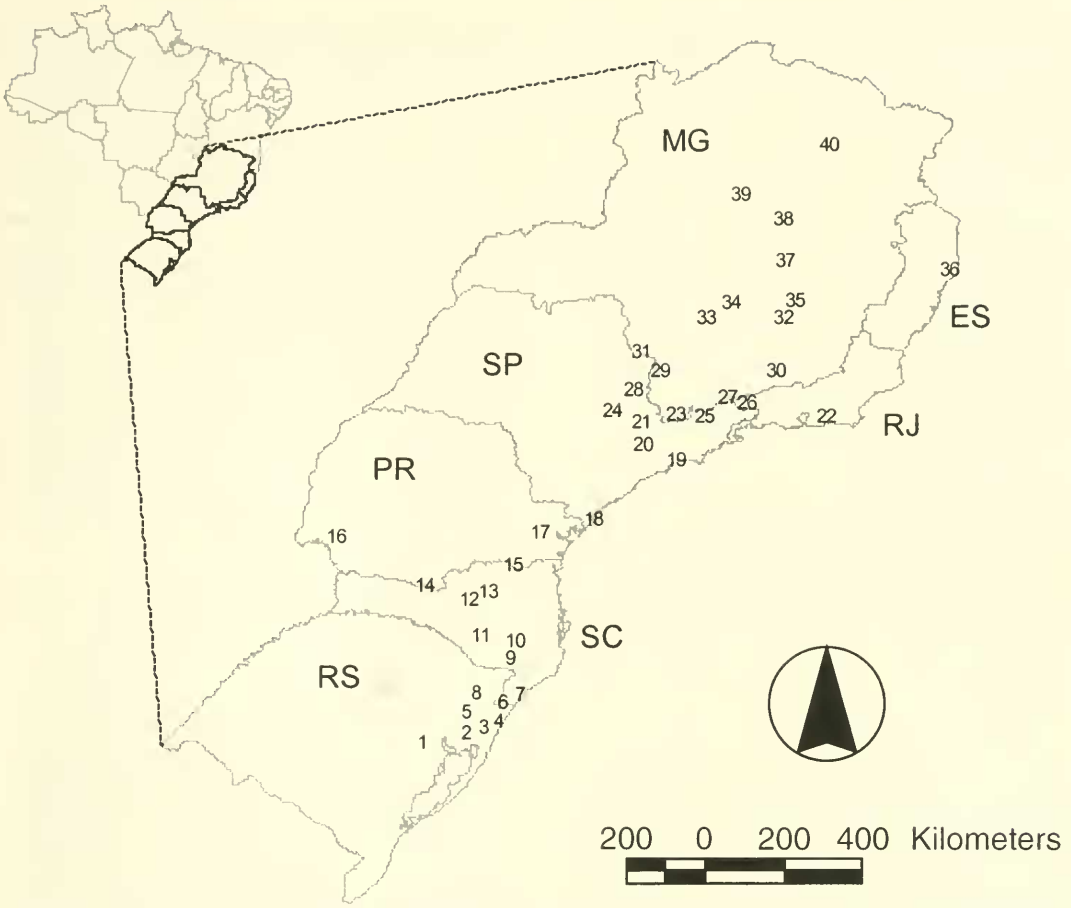

Fig. 1. States of southern and southeastern Brazil, with the localities where flowerheads were sampled. Abreviations of states: ES—Espírito Santo, MG—Minas Gerais, PR—Paraná, RJ—Rio de Janeiro, RS—Rio Grande do Sul, SC—Santa Catarina, SP—São Paulo. Localities and their code numbers are: Arceburgo, 31; Bertioga, 19; Bom Jardim da Serra, 9; Caçador, 13; Camanducaia, 23; Cambará do Sul, 8; Campinas, 21; Campos do Jordão, 25; Capão da Canoa, 3; Capão Novo, 4; Caraça, 35; Curitiba, 17; Diamantina, 38; Divinópolis, 34; Engenheiro Passos, 26; Formiga, 33; Grão Mogol, 40; Gravataí, 2; Guaíba, 1; Ilha do Cardoso, 18; Itatiaia, 26; Joaquim Felício (Serra do Cabral), 39; Jundiaí (Serra do Japi), 20; Lages, 11; Lauro Müller, 9; Lebon Régis, 12; Linhares, 36; Mafra, 15; Maquiné, 5; Maricá, 22; Matos Costa, 14; Mogi Guaçu, 28; Monte Verde, 23; Ouro Branco, 32; Parque Estadual de Ibitipoca, 30; Parque Nacional de Foz do Iguaçu, 16; Passa Quatro, 27; Pericó, 9; Piracicaba, 24; Poços de Caldas, 29; Praia Grande, 7; Santa Cecília, 12; Santo Antônio da Patrulha, 2; São Joaquim, 9; Serra do Cipó, 37; Visconde de Mauá, 26; Torres, 6; Urupema, 10. Some localities have the same number because they are not far enough to be represented as separate points in the map. See also Appendix II.

1997) in Serra do Japi, Jundiaí, São Paulo; and a survey of the endophages of the Tribe Eupatorieae in the Mantiqueira Mountain Range (Minas Gerais, São Paulo, and Rio de Janeiro) by Adriana Almeida and coworkers. Also, records of tephritids from sporadic samples of capitula obtained from 1989 to 1998 were added. Together, the records cover 48 localities from southern and southeastern Brazil (Fig. 1), comprising most of the region's main terrestrial habitats. Samples span all seasons, even though sampling was concentrated in the periods when most of the plant species are flowering, which varies between areas (summer and spring in southern areas, and summer and winter in southeastern areas). For the analysis of patterns of host use, species

richness, and geographical distribution, we also used data from Lewinsohn (1991), Foote (1980), Foote et al. (1993), Prado and Lewinsohn (1994) and Norrbom et al. (1999a, b).

In the host use analyses, plant species were recorded as "main hosts" only of tephritid species that were reared from more than one flowerhead sample, or for which more than five flies were reared from a single sample. Plant species from which we reared five or fewer flies from a single sample were conservatively classified as "occasional hosts."

In each locality, we inspected an average of four sites with a minimum distance of 500 m from each other, and sampled capitula in different developmental stages, from those bearing young flowers to those with mature achenes. Capitula in the pre-anthesis stage, very dry, or with dispersing achenes were excluded. Seventy per cent of the localities were visited more than once. The number of sampled capitula varied according to their size and the availability of the plant at each site, ranging from tens to several thousand. Most of the samples were standardized from 500 ml to 1,000 ml of fresh volume, whenever possible. We also sampled at least one voucher for each plant sample, for identification. The capitula were kept in transparent plastic pots of 500 ml or 1,300 ml, covered with a mesh cap, in which the adult insects emerged. In the laboratory, the rearing pots were inspected at regular intervals of one to four days to remove adults. Adults were kept in a refrigerator at 15°C for at least 24 hours so that they would develop their natural color before being preserved. After 15 days with no further insect emergence, rearing was concluded; this usually occurred six to eight weeks after collection.

Except for *Tomoplagia* species, which were largely identified by P. Prado, at least some specimens of all tephritid species were identified by A. L. Norrbom. Additional specimens were identified by keys from the literature or Norrbom manuscripts and comparison with the above specimens. Most Tephritidae specimens listed in this study are deposited in entomological collections of the Museu de História Natural da Universidade Estadual de Campinas and the Laboratório de Interações Insetos-Plantas from the Departamento de Zoologia of Universidade Estadual de Campinas. Selected specimens were also deposited in the Museu de Zoologia de São Paulo, São Paulo, Brazil, and in the National Museum of Natural History, Smithsonian Institution, Washington, DC. Host plant vouchers are deposited in the Herbário da Universidade Estadual de Campinas, and some duplicates in the National Museum of Natural History, Smithsonian Institution.

Results and Discussion

Characterization of the Fauna

We collected about 1,800 capitula samples from 403 Asteraceae species, comprising about 20% of the total described species for Brazil (Table 1). Taxonomically, this is a fairly unbiased sample of the Asteraceae regional flora—the proportion of sampled plant species did not vary much among tribes, ranging from 18% to 28% of described species of each tribe (Table 1). Endophagous tephritids emerged from 264 species of plants; these flies included a total of 80 tephritid species or morphospecies belonging to 18 genera (Tables 1–2).

Tephritidae is the most important family of endophagous insects feeding in Asteraceae capitula in Brazil. In our extensive survey of capitula endophages, they comprise 66% of the species, 55% of the genera, and 60% of the specimens, of all sampled insects. These results agree with lists of insect faunas from capitula in other world regions, in which tephritids are always among the most diverse and abundant families (Zwölfer 1982, 1988; Sobhian and Zwölfer 1985; Straw 1989a; Foote et al. 1993).

The largest Asteraceae tribes in Brazil also supported the greatest number of associated Tephritidae species (Table 1).

Table 1. Main Asteraceae tribes occurring in Brazil, and their numbers of described species, according to Barroso (1986). Other columns show, for each plant tribe, the number of sampled species in this study, the percentage of species with tephritid occurence, the total tephritid species number, and the number of tephritid species recorded exclusively in the tribe.

Asteraceae Tribe	No. Spp. in Brazil	No. Spp. Sampled	% Spp. with Tephritids	No. Spp. of Tephritidae	No. exclusive Spp. of Tephritidae
Astereae	203	37	46	14	6
Cardueae	17	3	0	0	0
Eupatorieae	616	147	52	28	6
Heliantheae	236	45	80	19	7
Inuleae[1]	56	10	20	3	3
Lactuceae	17	4	0	0	0
Mutisieae[2]	173	35	51	15	4
Senecioneae[3]	83	23	22	4	1
Helenieae	21	4	75	2	0
Vernonieae	442	125	82	40	24
TOTAL[4]	1,900	433	61	81	50

[1] Including the Pluchieae, Gnaphalieae and Inuleae s.s., separated subsequently as Tribes (Bremer 1994).
[2] Including the Barnadesioidea, separated subsequently as a subfamily (Bremer 1994).
[3] The only specimen of *Lamproxynella separata* we obtained was reared from one sample of *Senecio brasiliensis* (Speng.) Less. capitula, and is tentatively considered exclusive for Senecioneae.
[4] The total species for Brazil estimated by Barroso (1986) also includes the tribes Anthemideae, Calenduleae, and Cotuleae, from which we sampled no species.

Nonetheless, there are important differences between the two major tribes of Brazilian Asteraceae, Vernonieae and Eupatorieae. The Vernonieae have greater tephritid species richness and a greater proportion of plant species with these insects, despite the similar numbers of species in Brazil, and of the sampled species in these tribes (Table 1). The proportion of tephritid species exclusive to each tribe is also markedly greater among the Vernonieae, and very low in Eupatorieae (Table 1). Two possible non-exclusive explanations are that the Vernonieae are chemically and morphologically more distinct and/or were colonized by tephritid lineages intrinsically more specialized. The species from the main genera associated with Vernonieae (i.e., *Tomoplagia*, *Dictyotrypeta*, and *Tetreuaresta*), are normally restricted to related genera of host plants, in contrast to *Xanthaciura*, *Cecidochares* and *Trupanea* species, the most important genera associated with the tribe Eupatorieae. Five of the seven *Xanthaciura* species primarily associated with Eupatorieae occasionally use plants from the tribe Heliantheae, its sister group (Bremer 1994), and, more rarely, from the tribes Astereae and Vernonieae. Two of the three *Cecidochares* species have as an occasional host *Moquinia racemosa* (Spreng.) DC., which has a controversial tribal status but is not an Eupatorieae (Robinson 1994). Five of seven sampled *Trupanea* species may occur on Eupatorieae, but only one is exclusive to this tribe.

A notable exception to the general correlation of plant tribal diversity and tephritid diversity in southern Brazil is the virtual absence of endophagous tephritids on Senecioneae. From capitula samples of 22 Senecioneae species, we reared only one individual each of *Dioxyna chilensis* (Macquart), *Trypanaresta coelestina* (Hering), *Lamproxynella separata* (Malloch) (Appendix I), and *Trupanea* sp. The Senecioneae cannot be considered major hosts of any of these species, except perhaps *L. separata*, whose host range needs further investigation (see next section). In the Nearctic Region, capitula of Senecioneae are used by at least ten Tephritidae species in the genera

Table 2. Number of obtained Tephritidae specimens and species (described, undescribed and total), by genus. Total species exceeds the sum of described and undescribed species because it includes morphospecies of unclear taxonomic status (especially *Trupanea*). Also shown, the number of described species for each genus for the Neotropical Region (according to Norrbom et al. 1999a), and the tribes of the main host plants for each genus.

Genus	No. Specim.[1]	Descr. Spp.	Undescr. Spp.	Total Spp.	Neotrop. Spp.	Main Host Tribes
Acinia	37	3	0	3	9	Plucheeae
Acrotaeniini gen. 1	16	0	1	1		Vernonieae
Acrotaeniini gen. 2	31	0	1	1		Vernonieae
Acrotaeniini gen. 3	401	0	1	1		Mutisieae
Cecidochares	223	2	1	3	12	Eupatorieae
Dictyotrypeta	357	1	6	7	4	Vernonieae, Mutisieae, Heliantheae
Dioxyna	155	3	0	3	5	Heliantheae, Helenieae
Dyseuaresta	387	1	0	3	12	Heliantheae
Euarestoides	98	0	1	1	3	Mutisieae
Lamproxynela	1	1	0	1	8	Senecioneae
Neomyopites	105	1	1	2	28	Eupatorieae, Astereae
Paracantha	16	1	0	1	7	Heliantheae
Plaumannimyia	29	1	0	1	2	Astereae
Tetreuaresta	347	0	3	5	19	Vernonieae
Tomoplagia	3,375	12	13	25	45	Vernonieae[2]
Trupanea	713	0	0	8	80	Eupatorieae, Mutisieae
Trypanaresta	112	3	0	5	17	Astereae
Xanthaciura	3,294	6	3	9	17	Eupatorieae, Heliantheae
TOTAL	9,697	35	31	80	259	

[1] In order to show the relative importance of each genus, only specimens from extensive surveys (i.e., able to include all genera) are summed in this column.

[2] *Tomoplagia* is primarily associated with the tribe Vernonieae, but three species are specialists on other tribes: *T. costalimai* and *T. rivittata* (on Mutisieae), and *T. biseriata* (on Heliantheae).

Aciurina, *Stenopa*, *Tephritis*, *Trupanea*, and *Campiglossa* (Foote et al. 1993). Since the latter two genera also occur in the Neotropics, our finding of tephritid absence in Brazilian Senecioneae cannot be ascribed to the lack of colonizing groups. This absence might be attributed to the lower diversity of Senecioneae in Brazil compared to other important tribes (Table 1). However, in two tribes that are smaller and were less sampled than Senecioneae, tephritids are better represented (Table 1). In plants of the tribe Inuleae (genus *Pluchea*), we recorded three *Acinia* species (37 specimens) that are exclusive to this tribe (Table 2, and Appendix I). The only sampled genus of the tribe Helenieae, *Porophyllum*, includes main hosts of *Dioxyna chilensis* (16 specimens in *Porophyllum*, Appendix I) and an unidentified species of *Trupanea* (six specimens in *Porophyllum*). As already pointed out by Lewinsohn (1988), such scarcity of specialized tephritid species in Senecioneae is the first record of this nature for a whole Asteraceae tribe on a large geographical scale.

In Appendix I we list the 35 identified species, their host plants, and sample localities. One third of these species and three of the genera (*Acinia*, *Euarestoides*, and *Paracantha*) were not previously recorded for Brazil (Norrbom et al. 1999b).

The majority of the unidentified morphospecies are undescribed species, and they total a minimum of 31. The other species belong to genera whose species are difficult to identify because they are in need of systematic revision, especially *Trupanea*, *Trypanaresta* and *Dyseuaresta* (Foote et al. 1993). We also obtained three new genera, all belonging to the Tribe Acrotaeniini (Table 2), associated with endemic hosts of highland meadows on rocky outcrops (the Campo Rupestre vegetation, Giulietti and Pirani 1988). Also, the genus *Dictyotrypeta*,

as currently recognized, may be polyphyletic (Norrbom and Prado, unpublished data).

More than a third (31 of 80) of the species we obtained are undescribed, and this indicates how little known taxonomically neotropical tephritids still are. It also suggests that tephritid species richness is much higher than currently known. Extrapolating the ratio of 39% of new species we found to the total of tephritid species described for the Neotropical Region (716 spp., Norrbom et al. 1999a), we achieve an estimate of approximately 990 species, similar to the number of species currently recognized in the Afrotropical and Oriental Regions, considered today the areas with the greatest Tephritidae richness (Norrbom et al. 1999a). Although the number of described species in these regions presumably will rise with new occurrence data and new descriptions (e.g., see Freidberg and Norrbom 1999), the Neotropical Region is perhaps the least studied (Foote et al. 1993), and may have a larger portion of its fauna unknown.

The Tephritidae fauna of Asteraceae capitula in Brazil is dominated by the genus *Tomoplagia*, which comprises 31% of the morphospecies and 35% of the reared specimens (Table 2). *Xanthaciura* and *Trupanea* are, respectively, the second and third most important genera, both in species and in specimen numbers (Table 2). The genera *Dictyotrypeta*, *Tetreuaresta* and *Trypanaresta* follow, with five to seven morphospecies and two to four percent of the specimens each (Table 2). For the other 12 genera there are a maximum of three morphospecies each, and together they represent 17% of total specimens (Table 2). This fauna is predominantly Neotropical, except for the genera *Trupanea*, *Dioxyna* (with cosmopolitan distribution), and *Paracantha* (Panamerican). The other genera are Neotropical in origin, totaling 80% of the species and 90% of the obtained specimens. The genus *Acinia*, as currently recognized, includes Palearctic and American species, but according to Korneyev (1999) the latter are not closely related to the former and should be removed, thus this group of species should also be considered of Neotropical origin.

Although our survey is restricted to part of Brazil, we obtained an average of 30% of the number of recorded species of the Neotropics for each genus. For *Tomoplagia*, for example, we obtained 25 morphospecies compared with 45 described neotropical species (55%). Other important genera in our sample show a similar trend, such as *Xanthaciura* (9 morphospecies compared with 17 described ones), *Trypanaresta* (5:17), and *Tetreuaresta* (5:19). For all of these examples, the proportions are high because we obtained not only a representative percentage of the described species, but also many undescribed ones. In the genus *Dictyotrypeta*, for example, we obtained more morphospecies than the number of described ones (7:4). In contrast, the numbers of morphospecies of *Trupanea*, *Paracantha*, *Lamproxynella*, and *Neomyopites* in this study were small in relation to the total species recorded in the Neotropics (7–15%, see Table 2). It is very doubtful that these genera are associated with plant families other than Asteraceae in Brazil, but at least some of the species might develop in plant organs other than the flowerheads. There are few species of these genera recorded for Brazil (Norrbom et al. 1999b), however, and they probably are more diversified in other areas in the Neotropical Region.

The endophagous Tephritidae of capitula in southern Brazil are highly specialized. Sixty percent of the species were obtained from hosts belonging to a particular Asteraceae tribe or lower taxonomic category (Fig. 2). The main hosts for 80% of the species are restricted to a subtribe or lower category, and only 4% of the species have main hosts in more than one tribe. Oligophagy may be a general trend in the Tephritinae, since similar degrees of specialization were observed in the Nearctic and Palearctic Regions (Zwölfer 1982; Sobhian

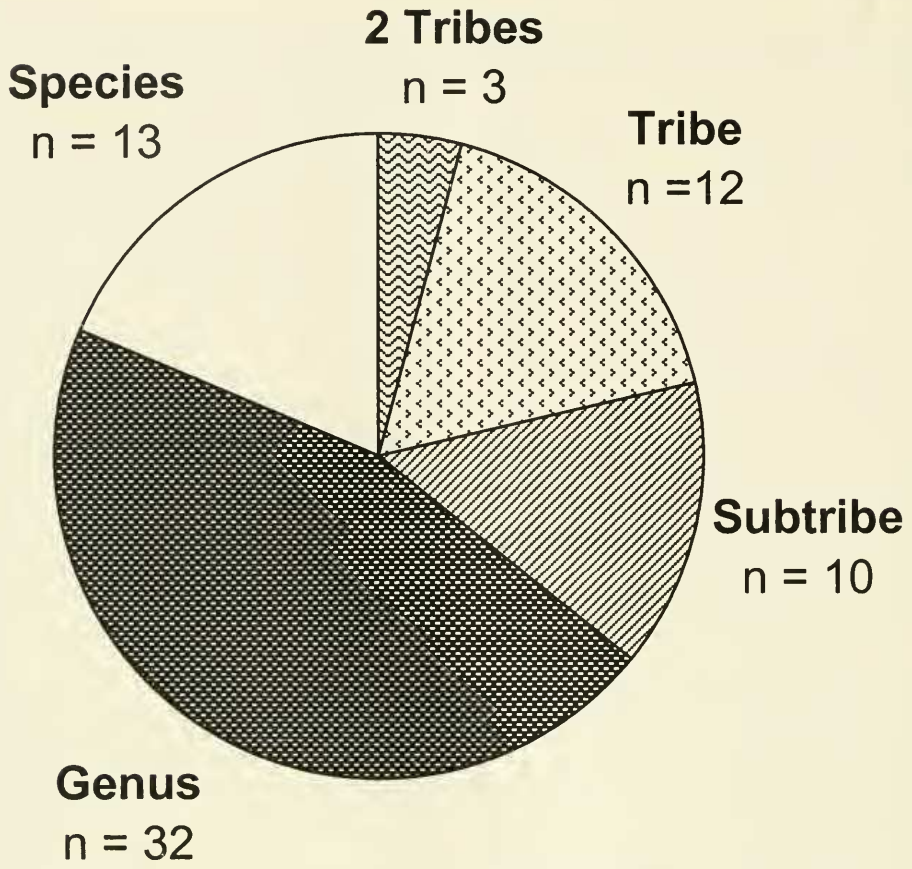

Fig. 2. Pie diagram of main host plant range of the obtained species of Tephritidae. Wedges represent the percentages of tephritid species reared from single host species, a single host genus, subtribe, or tribe, or from 2 tribes. Species reared from a single sample were excluded, because the data were too scarce to ascertain their host ranges.

and Zwölfer 1985; Goeden 1987, 1989, 1992, 1993, 1994, 1997; White and Elson-Harris 1992; Headrick and Goeden 1998). In the Tephritidae, capitula utilization depends on very specialized adaptations to the morphology, chemistry, and phenology of the host plant, which in general hinders the use of very different host plants (Zwölfer 1982, 1987; Straw 1989a, b). The genera of endophagous Tephritidae of capitula also are fairly specialized. Only three of the obtained genera have main host plants in more than two tribes. Two of these, *Tomoplagia* and *Dictyotrypeta*, are associated with three Asteraceae tribes, but are composed mostly of specialized species. *Tomoplagia* is mainly associated with one tribe (Vernonieae), with some species using plants from the tribes Mutisieae or Heliantheae. Among *Dictyotrypeta* species reared, two use plants of the related tribes Vernonieae and Mutisieae, two species are specialists on Heliantheae, and the remaining four species are associated with Vernonieae. Finally, *Trupanea* does in fact include many more generalist species and has been recorded from at least six different tribes of Asteraceae in other regions of the world (Munro 1964, Goeden 1992, White and Elson-Harris 1992, Foote et al. 1993). However, the genus is in dire need of revision, and host ranges of revised species may be smaller than they appear now.

As will be detailed in the next section,

host plant taxa for tephritid species and genera agree with the published records from other world regions and the scarce records for the Neotropics (Foote et al. 1993, Norrbom et al. 1999a). The small variation in the host plants used, even in different biogeographic regions, suggests that the set of potential hosts for a particular Tephritidae taxon is under strong phylogenetic restriction, as suggested by Zwölfer (1982, 1987), Straw (1989b), and Lewinsohn and Prado (in press).

Notes on the Obtained Genera

In the following discussion, the genera are arranged alphabetically, except for *Euarestoides* and *Plaumannimyia*, which are discussed with *Trypanaresta*.

The genus *Acinia* has 13 described species, widely distributed in the Americas and Palearctic Region (Norrbom et al. 1999a,b). However, Korneyev (1999) has indicated that the nine American (mainly Neotropical) species should be removed from the genus. We obtained specimens of *A. picturata* (Snow) and *A. ica* Hering from *Pluchea laxiflora* Hook. and Arn. ex. Baker, and of *A. aurata* Aczél from *Pluchea sagitalis* (Lam.) Cabrera (Appendix I). According to these records and those of Aczél (1958), Frías (1992) and Foote et al. (1993), hosts of *Acinia* in the New World are restricted to the tribe Plucheeae (Inuleae s. l.). No *Acinia* species was previously recorded for Brazil (Norrbom et al. 1999a, b), although Foote (1980, Table 1) indicated he had examined Brazilian specimens in a geographical distribution table of Neotropical genera.

Cecidochares is a mainly Neotropical genus, although *C. caliginosa* (Foote) (transferred from *Procecidocharoides* by Norrbom et al. 1999a, b) occurs in the southwestern United States and Mexico. There are 13 described species (Norrbom et al. 1999a, b), and at least 10 undescribed (Norrbom, unpublished). Specimens identified as *C. connexa* (Macquart) are referred to as '*C. connexa* complex' (See Appendix I), because recent biological evidence suggest that they may be a complex of cryptic species (McFadyen et al. pers. com.). The species of *Cecidochares* of known biology are all associated with Eupatorieae, and most are gall makers (Lima 1934, Silva et al. 1968, Cruttwell 1974, Foote et al. 1993). We reared three species of *Cecidochares* from capitula of the Tribe Eupatorieae, most of them without signs of galling. In one sample of *C. connexa* complex (from *Chromolaena laevigata* (Lam.) R. King and H. Rob., Paraná State), however, there were galls within the flower heads.

Dictyotrypeta is an exclusively Neotropical genus with numerous undescribed species (Foote 1980, Norrbom and Prado, unpubl.). Its limits are not well established, and it may be polyphyletic. The species reared in this study may not be congeneric with *D. syssema* Hendel, the type species (Norrbom and Prado, unpublished). The biology of the genus is poorly known; Foote et al. (1993) stated that four species breed in Heliantheae flowers. Of the seven *Dictyotrypeta* morphospecies we recorded, three use Vernonieae hosts (including *D. atacta* (Hendel), see Appendix I), two use Heliantheae, and two species use hosts from the tribes Vernonieae and Mutisieae.

Dioxyna is a broadly distributed genus with 13 described species. In the New World, their hosts are mainly species of the related tribes Heliantheae and Helenieae. The North American and Caribbean species, *D. picciola* (Bigot), is a relative generalist, using plants from the tribes Astereae, Heliantheae and Helenieae, whereas *D. thomae* (Curran) is recorded only from *Bidens bipinnata* L. and *Wedelia* sp. (Heliantheae) (Foote et al. 1993). In our surveys, all of the main hosts for *D. thomae* and *D. peregrina* (Loew) belong to the genus *Bidens*. The third species we obtained, *D. chilensis* (Marcquart), was reared from *Isostigma* sp. (Heliantheae) and *Porophyllum ruderale* (Jacq.) Cass. (Helenieae) (Appendix I).

Dyseuaresta is a little known, American,

mainly Neotropical genus (Foote 1980, Foote et al. 1993), with 12 described species (Norrbom et al. 1999a, b). Our data and records of *D. mexicana* (Wiedemann) from *Melanthera* spp. (Wasbauer 1972) suggest that this genus is primarily associated with the tribe Heliantheae. Frías (1992) reported *D. impluviata* (Blanchard) from *Senecio*, but this species may belong to *Lamproxynella*, a genus whose limits with *Dyseuaresta* are not well defined. We obtained *Dyseuaresta adelphica* (Hendel) from capitula of *Aspilia* spp. and from one species of *Calea* (Heliantheae). We reared two undescribed species, one from flowerheads of *Verbesina*, *Calea* and *Aspilia* (all Heliantheae), and the other from *Aspilia*, although both species occasionally used plants of the tribe Eupatorieae.

The genus *Lamproxynella* is exclusively Neotropical and is considered closely related to *Dyseuaresta* (Foote et al. 1993). Of eight described species, only *L. separata* (Malloch) is recorded from Brazil. We reared one specimen of this species from *Senecio brasiliensis* (Spreng.) Less. (Senecioneae) flowerheads (Appendix I). These data, and the rearing of two other species from Senecioneae in Chile (Norrbom, pers. obs.), are the only records of host plants of *Lamproxynella*, and suggest its association with the tribe Senecioneae.

The genus *Neomyopites*, which was recently proposed to include many of the New World species previously placed in *Urophora* (Freidberg and Norrbom 1999), has at least 28 described species, all but two of which are restricted to the Neotropical Region. Their known hosts belong to the tribes Astereae, Eupatorieae, Heliantheae, and Liabeae (Freidberg and Norrbom 1999). Some species induce galls in the capitula, as do many *Urophora* species in the Palearctic Region. We reared *N. paulensis* (Steyskal) from five Eupatorieae genera (Appendix I). This species is the main endophage of the genus *Mikania*, which is characterized by reduced capitula (with a maximum of four flowers), and has a poor endophagous fauna. The other species we obtained, which is probably undescribed, has a completely hyaline wing and was reared from only one sample of *Baccharis articulata* (Lam.) Pers. (Astereae). Both species were reared from normal capitula, with no sign of galling.

Paracantha is a genus restricted to the New World. Although five of its ten species occur in the Nearctic Region and can even reach southern Canada, the most closely related genera are all Neotropical (Foote et al. 1993). Until now, no species had been recorded for Brazil, although Foote (1980) indicated he had examined Brazilian specimens. The previously known hosts for *Paracantha* are from the genus *Cirsium* (tribe Cardueae) and several Heliantheae genera and species (Foote et al. 1993). We obtained individuals of *Paracantha australis* Malloch from five Heliantheae species from Minas Gerais, Rio Grande do Sul, and Santa Catarina (Appendix I). In Brazil, there are no native species of the tribe Cardueae, but three introduced species were sampled in southern Brazil (*Cirsium vulgare* (Savi) Ten., *Arctium minus* Bernh. and *Carduus nutans* L.). Although we collected a great volume of these plants in seven localities from Santa Catarina and Rio Grande do Sul, no *Paracantha* emerged from these samples.

Tetreuaresta is an exclusively Neotropical genus, with a great number of undescribed species (Foote 1980, Norrbom and Prado, unpublished). Its limits are not well established, and it may be polyphyletic. Biologically it is very poorly known, except for *Tetreuaresta obscuriventris* (Loew), introduced to Hawaii and other Pacific islands for control of its only known host plant, *Elephantopus mollis* H.B.K. (Vernonieae) (White and Elson-Harris 1992, Foote et al. 1993). The five *Tetreuaresta* species we obtained are all associated with Vernonieae hosts.

The Neotropical genus *Tomoplagia* has 47 described species (Norrbom et al. 1999a, b) and is primarily associated with the tribe

Vernonieae. Of the two species that occur in the United States, *T. obliqua* (Say) is recorded from at least seven Vernonieae species, and *T. cressoni* Aczél from *Trixis californica* Kellog and *Perezia microcephala* (DC.) A. Gray (Mutisieae) (Goeden and Headrick 1991, Foote et al. 1993). In Brazil, the association with Vernonieae had already been established (Lewinsohn 1988, Prado and Lewinsohn 1994), and *T. rudolphi* (Lutz and Lima) had been recorded making stem galls on *Vernonanthura* spp. (Lima 1934, Silva et al. 1968). The main hosts for all the species of *Tomoplagia* we obtained belong to this tribe, with three exceptions, namely, *T. costalimai* Aczél, which uses *Trixis* spp. (Tribe Mutisieae), *T. trivittata* (Lutz and Lima), which uses *Gochnatia* spp. (Mutisieae), and *T. biseriata* (Loew), which uses *Calea* spp. (Heliantheae) (Appendix 1). Plants of the tribes Mutisieae and Heliantheae are occasionally used by some other *Tomoplagia* species (Appendix 1). Therefore, the occasional use of Heliantheae and Mutisieae by an ancestor may have facilitated the evolution of the species specialized on these tribes.

Most species of *Tomoplagia* are restricted to only one tribe or to a lower taxonomic category of host plants. However, the most polyphagous species, *T. incompleta* (Williston), may occasionally use Mutisieae and Eupatorieae as hosts, apart from its Vernonieae main hosts (Appendix 1, Prado and Lewinsohn 1994). *Tomoplagia* belongs to the mostly Neotropical tribe Acrotaeniini (Norrbom 1987, Foote et al. 1993, but see also Korneyev 1999). The known host plants for other Acrotaeniini (genera *Tetreuaresta* and *Acrotaenia*) belong to the tribes Vernonieae and Heliantheae (Foote et al. 1993, Appendix 1). Among the Vernonieae, the subtribe Lychnophorinae is virtually endemic to montane rocky outcrops, with greatest diversity in the Serra do Espinhaço in Minas Gerais (Robinson et al. 1980, Robinson 1992, Bremer 1994). In this study, we obtained six new *Tomoplagia* species specialized on this subtribe. These species had not been sampled before and are associated with plants with limited distributions, hence they are also probably endemic to rocky outcrops (Prado et al., unpublished). We also obtained two species from two new genera of Acrotaeniini. One of these species uses *Lychnophora* spp., a genus restricted to highland meadows on rocky outcrops (campos rupestres) and adjacent Brazilian savannas (cerrados) from Minas Gerais, Bahia and Goiás (Coile and Jones 1981, Robinson et al. 1980, Robinson 1992). The other species was recorded from species of *Lychnophora* and *Eremanthus*, a genus found in campo rupestre and cerrado vegetation from central and southeastern Brazil (MacLeish 1987). About 400 specimens of a third Acrotaeniini genus were reared from capitula of *Wunderlichia mirabilis* Riedel (Mutisieae), a primitive Asteraceae also restricted to rocky outcrops of central Brazil (Bremer 1994).

Trupanea is one of the largest genera of Tephritinae, with more than 200 described species, including 80 in the Neotropical Region (Norrbom et al. 1999a, b). Species identification in this genus is extremely difficult, and the Neotropical fauna lacks an adequate taxonomic revision (Foote 1980, Foote et al. 1993). In a preliminary examination, we separated our *Trupanea* specimens into eight morphospecies that are mainly associated with the tribes Eupatorieae and Mutisieae. One morphospecies was also reared from *Porophyllum* (tribe Helenieae, formerly placed in the Heliantheae). The known hosts for *Trupanea* in the Nearctic Region belong to these three tribes (Wasbauer 1972; Goeden 1985, 1992; Foote et al. 1993). In Chile, the genus is recorded from the tribes Astereae and Heliantheae (Frías 1985). In the present study, the majority of *Trupanea* morphospecies had broader host ranges than the species of the other tephritid genera. Four morphospecies were recorded from two to five Asteraceae tribes.

Trypanaresta is a genus of Neotropical origin, with 17 described species (Norrbom

et al. 1999a, b). The synonymy of *Euarestoides arnaudi* Foote with *E. flavus* (Adams) and its transfer to *Trypanaresta* (Norrbom et al. 1999b) expanded the known distribution of the genus to the Nearctic Region. *Trypanaresta* is closely related to *Plaumannimyia* (which has two described species, restricted to southern Brazil) and *Euarestoides* (three species in Central America, Mexico, and USA) (Norrbom et al. 1999a, b). Species of the tribe Astereae, mainly of the genus *Baccharis*, are recorded in the literature as hosts for the first two genera (Foote et al. 1993), which is in accord with our data. The two more abundant species of *Trypanaresta* in our surveys, *T. coelestina* (Hering) and *T. imitatrix* (Hering), were obtained from various *Baccharis* species (Appendix I), from either male or female flowers. The three remaining species were obtained in small numbers, and from few samples, also from Astereae. One individual of *T. thomsoni* (Hendel) was reared from capitula of *Solidago chilensis* Meyen (Appendix I), two individuals of an unidentified species were reared from *Conyza* spp. and *S. chilensis* capitula, and two individuals of another unidentified species were reared from capitula of *Conyza bonariensis* (L.) Cronquist (all in Astereae). We also obtained ten individuals of *Plaumannimyia pallens* Hering from capitula of *Baccharis* spp. in southern Brazil (Appendix I). In the genus *Euarestoides*, only the hosts of *E. acutangulus* (Thomson) were previously known, and these include species of the tribes Heliantheae, Helenieae and Astereae (Foote et al. 1993). In the present study, we obtained one undescribed species of *Euarestoides* from capitula of four species of *Gochnatia* (Mutisieae) from Minas Gerais and Rio de Janeiro. *Euarestoides* was not previously recorded from Brazil (Norrbom et al. 1999b).

Xanthaciura is a Neotropical and Nearctic genus with 17 described species (Norrbom et al. 1999a, b). It is known from the central, southeastern, southern and northeastern regions of Brazil and is associated with the tribes Heliantheae and Eupatorieae. The few published host plant data refer to three of the four species that reach the United States, *X. connexionis* Benjamin, *X. insecta* (Loew), and *X. tetraspina* (Phillips) (Foote et al. 1993), and their host plant tribes and genera are the same as presented in this study. The fourth species that reaches the United States, *X. chrysura* (Thomson), had no previously reported host plants (Foote et al. 1993). We recorded nine *Xanthaciura* species from Asteraceae capitula, three of them undescribed (Table 2). The most abundant species in our samples were *X. biocellata* (Thomson) and *X. chrysura*, both primarily associated with various genera of Eupatorieae (Appendix I). *Xanthaciura quadrisetosa* (Hendel), *X. mallochi* Aczél, and the three undescribed species are also primarily associated with Eupatorieae. *Xanthaciura insecta* (Loew) is primarily associated with the subtribe Coreopsidinae of the tribe Heliantheae, as shown by our records from *Bidens* spp. (Appendix I), and those of Wasbauer (1972) from *Bidens* spp. in the United States, and of Norrbom (in Foote et al. 1993) from *Bidens squarrosa* Kunth in Venezuela and *Dahlia coccinea* Cav. in Mexico. *Xanthaciura unipuncta* Malloch is also associated with Heliantheae, but also breeds in some species of Eupatorieae (Appendix I).

Acknowledgments

This work was supported by Fapesp, CNPq, FAEP/Unicamp (Brazil), and the Smithsonian Institution and USDA/ARS (USA). Adalberto dos Santos, Flávia Batista, Vinicius Motta, Gabrielle Althausen, and José Carlos da Silva (Unicamp) provided invaluable assistance in field and laboratory work. Our thanks also to João Semir, John Pruski, Nelson Matzenbacher, Harold Robinson, and the late Hermógenes Leitão Filho for plant identification; and to Ângelo do Pires Prado for assistance in tephritid systematics and comments on drafts of this paper. John W. Brown, Amnon Freidberg, and Norman Woodley also kindly reviewed

the manuscript. Field lodging at Diamantina was provided by the Centro Eschwege de Geologia, Universidade Federal de Minas Gerais. Special thanks are due to Nelson Matzenbacher, Rogério P. Martins, and Francisco Prado, and their families, who kindly provided housing during part of our field trips.

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Appendix 1

Checklist of Described Tephritid Species Reared from Asteraceae Capitula in Southern and Southeastern Brazil

This appendix lists the described species obtained in our survey, their hosts, and sample sites. We also in-

dicate the number of individuals of each species we obtained and the number of samples from which they were reared. Nomenclature and geographical distributions are in accord with Norrbom et al. (1999b). Localities are grouped by states, which are indicated by their abbreviations. Host plants are grouped by tribe. Plant species from which fewer than five tephritid individuals were reared from a single sample were conservatively considered occasional hosts. For a map of localities see Fig. 1, and for a list of them see Appendix II. For full scientific names of host plants, see Appendix III.

Acinia aurata Aczél
2 samples, 2 individuals.
Localities: SP: Bertioga, Campinas.
Previously known distribution: Bolivia, Argentina.
Main host: Inuleae: *Pluchea sagitalis.*

Acinia ica Hering
1 sample, 30 individuals.
Locality: MG: Ouro Branco.
Previously known distribution: Peru.
Main host: Inuleae: *Pluchea laxiflora.*

Acinia picturata (Snow)
1 sample, 5 individuals.
Locality: SC: Matos Costa.
Previously known distribution: USA, S to Guatemala, West Indies, Hawaii (introd.).
Main host: Inuleae: *Pluchea laxiflora.*

Cecidochares connexa (Macquart) complex
15 samples, 45 individuals.
Localities: MG: Camanducaia, Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Parque Estadual de Ibitipoca, Serra do Cipó, RJ: Visconde de Mauá.
Previously known distribution: Venezuela, Argentina, Brazil.
Main hosts: Eupatorieae: *Chromolaena chaseae, Chromolaena cylindrocephala, Chromolaena squalida, Pseudobrickellia brasiliensis.*
Occasional hosts: Eupatorieae: *Chromolaena ascendens, Chromolaena maximilianii, Chromolaena multiflosculosa, Chromolaena sp., Trichogonia salviaefolia, Trichogonia villosa,* Moquinieae: *Moquinia racemosa.*

Cecidochares fluminensis (Lima)
11 samples, 51 individuals.
Localities: MG: Monte Verde, Parque Estadual de Ibitipoca, Passa Quatro, RJ: Itatiaia, Visconde de Mauá, SP: Campinas, Campos do Jordão.
Previously known distribution: Central America, Trinidad, Venezuela, Guyana, Brazil (AM, RO, RJ, SP).
Main hosts: Eupatorieae: *Chromolaena maximilianii, Chromolaena laevigata.*
Occasional hosts: Eupatorieae: *Chromolaena hookeriana*

Dictyotrypeta atacta (Hendel)
8 samples, 192 individuals.
Localities: MG: Diamantina, Joaquim Felício (Serra do Cabral), Serra do Cipó.
Previously known distribution: Brazil, Paraguay.
Main hosts: Vernonieae: *Lessingianthus buddleiifolius, Lessingianthus coriaceus, Lessingianthus roseus, Lessingianthus vepretorum.*
Occasional hosts: Vernonieae: *Proteopsis argentea,* Eupatorieae: *Trichogonia villosa.*

Dioxyna chilensis (Macquart)
7 samples, 77 individuals.
Localities: MG: Diamantina, Joaquim Felício (Serra do Cabral), RS: Guaíba, SP: Campinas.
Previously known distribution: Peru, Bolivia, Chile, Argentina.
Main hosts: Heliantheae: *Isostigma* sp., Helenieae: *Porophyllum ruderale.*
Occasional hosts: Heliantheae: *Calea graminifolia,* Helenieae: *Porophyllum riedelii,* Senecioneae: *Senecio oxyphyllus.*

Dioxyna peregrina (Loew)
7 samples, 26 individuals.
Localities: MG: Passa Quatro, SP: Bertioga, Campinas, Campos do Jordão, Jundiaí (Serra do Japi).
Previously known distribution: Brazil
Main host: Heliantheae: *Bidens pilosa.*
Occasional host: Eupatorieae: *Praxelis clematidea.*

Dioxyna thomae (Curran)
3 samples, 39 individuals.
Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral).
Previously known distribution: U.S.A. (Florida), West Indies, Guyana.
Main hosts: Heliantheae: *Bidens* spp. (two species).

Dyseuaresta adelphica (Hendel)
23 samples, 202 individuals.
Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, Serra do Cipó.
Previously known distribution: Brazil (MS, PR), Paraguay.
Main hosts: Heliantheae: *Aspilia jolyana, Aspilia cylindrocephala, Aspilia laevissima,* six other undetemined species of *Aspilia.*
Occasional hosts: Heliantheae: *Aspilia foliacea,* two other undetemined species of *Aspilia* spp., *Calea* sp.

Lamproxynella separata (Malloch)
1 sample, 1 individual.
Locality: MG: Poços de Caldas.
Previously known distribution: Brazil (SP), Argentina.
Host: Senecioneae: *Senecio brasiliensis.*

Neomyopites paulensis (Steyskal)
37 samples, 130 individuals.
Localities: MG: Camanducaia, Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, Parque Estadual de Ibitipoca, Passa Quatro, Ser-

ra do Cipó, RJ: Maricá, Visconde de Mauá, SC: Lages, Mafra, SP: Bertioga, Campinas, Campos do Jordão.

Previously known distribution: Trinidad, Paraguay, Brazil (SP).

Main hosts: Eupatorieae: *Ayapana amigdalina, Chromolaena laevigata, Chromolaena maximilianii, Chromolaena squalida, Grazielia intermedia, Mikania cipoensis, Mikania micrantha, Mikania officinalis, Mikania sessilifolia, Praxelis clematidea, Stomathanthes polycephalus, Symphyopappus decussatus.*

Occasional hosts: Eupatorieae: *Chromolaena chaseae, Chromolaena odorata, Mikania retifolia, Mikania sp., Pseudobrickellia brasiliensis.*

Paracantha australis Malloch

5 samples, 16 individuals.

Localities: MG: Serra do Cipó, Diamantina, RS: Cambará do Sul, SC: Bom Jardim da Serra, Lages.

Previously known distribution: Argentina, Uruguay.

Main hosts: Heliantheae: *Calea* spp. (at least three species).

Occasional hosts: Heliantheae: *Aspilia* sp., *Verbesina subcordata.*

Plaumanniinyia pallens Hering

4 samples, 10 individuals.

Localities: RS: Guaíba, SC: Lages, Matos Costa, Pericó.

Previously known distribution: Brazil (SC).

Main hosts: Astereae: *Baccharis dracunculifolia, Baccharis punctulata, Baccharis uncinella, Baccharis* spp. (at least two other species).

Tomoplagia argentiniensis Aczél

39 samples, 300 individuals.

Localities: ES: Linhares, MG: Serra do Cipó, Ouro Branco, RJ: Itatiaia, SP: Campinas, Ilha do Cardoso, Jundiaí (Serra do Japi).

Previously known distribution: Brazil (MG, RJ, SP), Argentina.

Main host: Vernonieae: *Cyrtocymura scorpioides.*

Tomoplagia biseriata (Loew)

4 samples, 29 individuals.

Localities: MG: Diamantina, Grão Mogol, SC: Lages.

Previously known distribution: Ecuador, Brazil.

Main hosts: Heliantheae: *Calea nitida, Calea oxyleps, Calea* spp. (at least two other species).

Tomoplagia costalimai Aczél

16 samples, 83 individuals.

Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Serra do Cipó, RS: Guaíba, SC: Lages, Matos Costa, SP: Jundiaí (Serra do Japi).

Previously known distribution: Argentina.

Main hosts: Mutisieae: *Trixis mollissima, Trixis praestans, Trixis vauthieri, Trixis verbasciformis.*

Occasional hosts: Mutisieae: *Jungia floribunda.*

Tomoplagia fiebrigi Hendel

5 samples, 46 individuals.

Localities: MG: Joaquim Felício (Serra do Cabral), RS: Guaíba, SC: Lages.

Previously known distribution: Paraguay, Argentina.

Main hosts: Vernonieae: *Vernonanthura aff. lucida, Vernonanthura nudiflora.*

Occasional host: Vernonieae: *Vernonanthura tweedieana.*

Tomoplagia formosa Aczél

13 samples, 45 individuals.

Localities: MG: Caraça, Diamantina, Serra do Cipó, PR: 20 km SE of Curitiba, RJ: Visconde de Mauá, RS: Guaíba, SC: Bom Jardim da Serra, Lages, São Joaquim.

Previously known distribution: Brazil (MG), Argentina.

Main hosts: Vernonieae: *Chrysolaena flexuosa, Chrysolaena platensis, Lepidaploa salzmanii.*

Occasional hosts: Vernonieae: *Chrysolaena herbacea, Lessingianthus (Oligocephalus) desertorum,* Heliantheae: *Verbesina* sp.

Tomoplagia incompleta (Williston)

132 samples, 512 individuals.

Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Passa Quatro, Ouro Branco, Serra do Cipó, RJ: Itatiaia, RS: Capão Novo, Guaíba, SC: Bom Jardim da Serra, Lages, Mafra, Pericó.

Previously known distribution: West Indies, Paraguay, Brazil (MG), Argentina.

Main hosts: Vernonieae: *Chresta sphaerocephala, Chrysolaena flexuosa, Chrysolaena herbacea, Chrysolaena platensis, Echinochoryne schwenkiaefolia, Lepidaploa lilacina, Lepidaploa spixiana, Lepidaploa salzmanii, Lessingianthus (Oligocephalus) simplex, Lessingianthus carduoides, Lessingianthus linearis, Lessingianthus linearifolius, Lessingianthus psilophyllus, Lessingianthus pumillus, Lessingianthus roseus, Lessingianthus stoechas, Lessingianthus vepretorum.*

Occasional hosts: Eupatorieae: *Chromolaena laevigata, Heterocondylus alatus, Mikania sessilifolia,* Mutisieae: *Gochnatia amplexifolia, Trixis vauthieri,* Vernonieae: *Chresta* sp., *Eremanthus* sp., *Lepidaploa* sp., *Lessingianthus (Oligocephalus) desertorum, Lessingianthus brevipetiolatus, Lessingianthus coriaceus, Lessingianthus glabratus, Lessingianthus laevigatus, Lessingianthus poliphyllus, Lessingianthus rubricaulis, Lessingianthus sellowii, Lessingianthus warmingianus, Minasia* sp., *Vernonia incana, Vernonanthura glanduloso-dentata.*

Tomoplagia minuta Hering

48 samples, 648 individuals.

Localities: MG: Diamantina, Formiga, Grão Mogol, Monte Verde, Ouro Branco, Parque Estadual de Ibitipoca, Serra do Cipó, RJ: Itatiaia, Visconde de

Mauá, RS: Cambará do Sul, SC: Lages, Matos Costa, Mafra.
Previously known distribution: Brazil (MG, SP, SC).
Main hosts: Vernonieae: *Vernonanthura beyrichi, Vernonanthura catharinensis, Vernonanthura chamaedrys, Vernonanthura mariana, Vernonanthura membranacea, Vernonanthura montevidensis, Vernonanthura phaeoneura, Vernonanthura phosphorica, Vernonanthura subverticillata, Vernonanthura westiniana.*
Occasional host: Vernonieae: *Vernonanthura petiolaris, Vernonanthura tweedieana.*

Tomoplagia punctata Aczél
7 samples, 27 individuals.
Localities: MG: Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, RJ: Itatiaia, Visconde de Mauá, SP: Bertioga.
Previously known distribution: Argentina.
Main host: Vernonieae: *Centratherum punctatum.*

Tomoplagia pseudopenicillata Aczél
14 samples, 55 individuals.
Localities: MG: Ouro Branco, Serra do Cipó, SP: Ilha do Cardoso, Campinas.
Previously known distribution: Brazil (MG, SP).
Main host: Vernonieae: *Cyrtocymura scorpioides.*

Tomoplagia reimoseri Hendel
57 samples, 1093 individuals.
Localities: MG: Diamantina, Formiga, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco Serra do Cipó.
Previously known distribution: Trinidad, Venezuela, Paraguay, Brazil, Argentina.
Main hosts: Vernonieae: *Vernonanthura glandulosodentata, Vernonanthura mariana, Vernonanthura membranacea, Vernonanthura mucronulata, Vernonanthura phosphorica, Vernonanthura subverticillata, Vernonanthura* spp. (at least two other species).
Occasional hosts: Astereae: *Baccharis aphylla,* Vernonieae: *Cyrtocymura scorpioides, Minasia* sp.

Tomoplagia tripunctata Hendel
56 samples, 133 individuals.
Localities: MG: Caraça, Diamantina, Ouro Branco, Parque Estadual de Ibitipoca, Serra do Cipó.
Previously known distribution: Paraguay, Brazil.
Main hosts: Vernonieae: *Lessingianthus brevipetiolatus, Lessingianthus carduoides, Lessingianthus linearifolius, Lessingianthus linearis, Lessingianthus psilophyllus, Lessingianthus roseus, Lessingianthus vepretorum.*
Occasional hosts: Mutisieae: *Trixis vauthieri,* Vernonieae: *Lessingianthus pumillus, Lessingianthus rosmarinifolius, Lessingianthus stoechas, Lessingianthus pycnostachyus.*

Tomoplagia trivittata (Lutz & Lima)
2 samples, 14 individuals.
Localities: MG: Joaquim Felício (Serra do Cabral), SP: Mogi Guaçu.
Previously known distribution: Brazil (MG, SP, MS), Argentina.
Main hosts: Mutisieae: *Gochnatia barrosii, Gochnatia floribunda.*

Trypanaresta coelestina (Hering)
14 samples, 76 individuals.
Localities: MG: Diamantina, Ouro Branco, Passa Quatro, Serra do Cipó, PR: 25 km SE of Curitiba, RS: Cambará do Sul, Santo Antônio da Patrulha, SC: Lages.
Previously known distribution: Brazil (PR, SC).
Main hosts: Astereae: *Baccharis dracunculifolia, Baccharis helichrysoides, Baccharis leucopappa, Baccharis brachylaenoides* var. *ligustrina, Baccharis trinervis.*
Occasional hosts: Astereae: *Baccharis brachylaenoides, Baccharis ramosissima, Baccharis serrulata,* Senecioneae: *Senecio selloi.*

Trypanaresta imitatrix (Hering)
6 samples, 11 individuals.
Localities: MG: Ouro Branco, Serra do Cipó, PR: Parque Nacional de Foz do Iguaçu, RS: Guaíba, SP: Campinas.
Previously known distribution: Brazil (SP to SC), Argentina.
Main hosts: Astereae: *Baccharis dracunculifolia, Baccharis punctulata, Baccharis trinervis, Heterothalamus psiadioides.*

Trypanaresta thomsoni (Hendel)
8 samples, 12 individuals.
Localities: RJ: Maricá, SC: Santa Cecília, SP: Bertioga, Campinas.
Previously known distribution: Bolivia, Argentina.
Main hosts: Astereae: *Conyza canadensis, Conyza bonariensis.*
Occasional hosts: Astereae: *Solidago chilensis,* Inuleae: *Pluchea sagitalis.*

Xanthaciura biocellata (Thomson)
165 samples, 1,506 individuals.
Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, Parque Estadual de Ibitipoca, Passa Quatro, Serra do Cipó, RJ: Engenheiro Passos, Itatiaia, Maricá, Visconde de Mauá, RS: Gravataí, SP: Bertioga, Campinas, Campos do Jordão.
Previously known distribution: Peru, Bolivia, Paraguay, Brazil, Uruguay, Argentina.
Main hosts: Eupatorieae: *Ageratum fastigiatum, Ayapana amigdalina, Barrosoa betonicaeformis, Chromolaena barbacensis, Chromolaena chaseae, Chromolaena costatipes, Chromolaena cylindrocephala, Chromolaena decumbens, Chromolaena hookeriana, Chromolaena horminoides, Chromolaena laevigata, Chromolaena maximilianii, Chromolaena minasgeraesensis, Chromolaena pedalis,*

Chromolaena pungens, Chromolaena sagittifera, Chromolaena squalida, Heterocondylus alatus, Heterocondylus amphidictyus, Heterocondylus jaraguensis, Koanophyllon adamantium, Praxelis clematidea, Symphyopappus cuneatus, Symphyopappus decussatus, Trichogonia hirtiflora, Trichogonia salviaefolia, Trichogonia villosa, Trichogoniopsis adenantha.

Occasional hosts: Eupatorieae: *Acritopappus longifolius, Pseudobrickellia brasiliensis, Campuloclinium campuloclinoides, Campuloclinium chlorolepsis, Campuloclinium macrocephalum, Campuloclinium megacephalum, Chromolaena congesta, Chromolaena matogrossensis, Chromolaena multiflosculosa, Chromolaena myriocephala, Chromolaena odorata, Chromolaena stachyophylla, Symphyopappus reticulatus, Symphyopappus* aff. *reticulatus,* Mutisieae: *Inulopsis scaposa,* Vernonieae: *Lessingianthus (Oligocephalus) virgulatus, Lessingianthus hovaefolius, Lychnophora* sp., *Vernonanthura mariana.*

Xanthaciura chrysura (Thomson)

167 samples, 829 individuals.

Localities: MG: Arceburgo, Camanducaia, Caraça, Diamantina, between Formiga e Divinópolis, Grão Mogol, Joaquim Felício (Serra do Cabral), Monte Verde, Ouro Branco, Parque Estadual de Ibitipoca, Passa Quatro, Serra do Cipó, RJ: Engenheiro Passos, Itatiaia, Visconde de Mauá, RS: Cambará do Sul, Guaíba, Gravataí, SC: Bom Jardim da Serra, Lages, Matos Costa, Mafra, Pericó, SP: Bertioga, Campinas, Campos do Jordão, Ilha do Cardoso, Ilha Comprida, Jundiaí (Serra do Japi).

Previously known distribution: USA (Florida), from Mexico to Argentina.

Main hosts: Eupatorieae: *Adenostemma lavenia, Ageratum conyzoides, Ageratum fastigiatum, Ageratum* sp., *Austroeupatorium inulaefolium, Austroeupatorium paulinum, Austroeupatorium silphiifolium, Barrosoa betonicaeformis, Campovassouria cruciata, Campuloclinium macrocephalum, Campuloclinium purpurascens, Chromolaena chaseae, Chromolaena cylindrocephala, Chromolaena horminoides, Chromolaena laevigata, Chromolaena maximilianii, Chromolaena minasgeraesensis, Chromolaena pungens, Chromolaena squalida, Hatschbachiella tweedieana, Heterocondylus alatus, Heterocondylus grandis, Heterocondylus jaraguensis, Grazielia gaudichaudeana, Grazilellia intermedia, Praxelis clematidea, Trichogonia hirtiflora, Trichogoniopsis adenantha.*

Occasional hosts: *Austroeupatorium picturatum, Chromolaena barbacensis, Chromolaena hookeriana, Chromolaena matogrossensis, Chromolaena multiflosculosa, Chromolaena myriocephala, Chromolaena pedalis, Chromolaena* spp. (at least three other species), *Grazielia* sp., *Koanophyllon thysanolepis, Mikania cipoensis, Mikania cordifolia, Mikania decumbens, Mikania lasiandrae, Mikania micrantha, Mikania officinalis, Mikania sessilifolia, Symphyopappus decussatus, Symphyopappus itatiayensis, Vittetia orbiculata,* Heliantheae: *Aspilia pascalioides,* Vernonieae: *Eremanthus* sp.

Xanthaciura insecta (Loew)

3 samples, 31 individuals.

Localities: MG: Diamantina, Joaquim Felício (Serra do Cabral), Ouro Branco.

Previously known distribution: USA, Mexico to Venezuela, West Indies.

Main hosts: Heliantheae: *Bidens brasiliensis, Bidens* sp.

Xanthaciura mallochi Aczél

3 samples, 10 individuals.

Localities: MG: Parque Estadual de Ibitipoca.

Previously known distribution: Costa Rica, Panama, Colobia, Ecuador, Peru, n. Argentina, s. Brazil.

Main host: Eupatorieae: *Chromolaena maximilianii.*

Xanthaciura quadrisetosa (Hendel)

27 samples, 51 individuals.

Localities: MG: Diamantina, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, Parque Estadual de Ibitipoca, Passa Quatro, RS: Capão Novo, SC: Lages, RJ: Visconde de Mauá, SP: Campos do Jordão, Piracicaba.

Previously known distribution: Bolivia, Brazil, Argentina.

Main hosts: Eupatorieae: *Ageratum conyzoides, Ageratum fastigiatum, Campovassouria cruciata, Koanophyllon thysanolepis, Mikania purpurascens.*

Occasional hosts: Eupatorieae: *Austroeupatorium* sp., *Grazielia intermedia, Symphyopappus casarettoi,* Heliantheae: *Bidens* sp., *Calea nitida.*

Xanthaciura unipuncta Malloch

22 samples, 79 individuals.

Localities: MG: Diamantina, Guaíba, Grão Mogol, Joaquim Felício (Serra do Cabral), Ouro Branco, Serra do Cipó, RJ: Engenheiro Passos, Maricá, SC: Lages, Pericá, SC: Lages, Pericó, SP: Bertioga, Campinas.

Previously known distribution: Guatemala to Colombia and Trinidad, Paraguay, Brazil, Argentina.

Main hosts: Eupatorieae: *Campovassouria cruciata,* Heliantheae: *Aspilia cylindrocephala, Aspilia jolyana, Aspilia* spp. (at least four species), *Wedelia paludosa.*

Occasional hosts: Astereae: *Baccharis punctulata,* Eupatorieae: *Barrosoa betonicaeformis, Chromolaena squalida, Mikania purpurascens, Trichogonia villosa,* Heliantheae: *Aspilia montevidensis, Calea elongata, Calea* sp. Vernonieae: *Cyrtocymura scorpioides.*

Appendix II
Gazetteer

This appendix lists the sites sampled in this study and their state (ES—Espírito Santo; MG—Minas Gerais; PR—Paraná; RJ—Rio de Janeiro; RS—Rio Grande do Sul; SC—Santa Catarina; SP—São Paulo), their code number in Fig. 1, and their geographical coordinates. Some localities have the same code number because they are not far enough apart to be represented as separate points in the map in Fig. 1.

Code	Locality	State	Coordinates
1	Guaíba	RS	30°11′S51°51′W
2	Gravataí	RS	29°55′S50°50′W
2	Santo Antônio da Patrulha	RS	29°53′S50°50′W
3	Capão da Canoa	RS	29°42′S50°20′W
4	Capão Novo	RS	29°41′S49°49′W
5	Maquiné	RS	29°30′S50°50′W
6	Torres	RS	29°23′S49°49′W
7	Praia Grande	SC	29°11′S49°49′W
8	Cambará do Sul	RS	29°04′S50°38′W
9	Bom Jardim da Serra	SC	28°18′S49°49′W
9	Lauro Müller	SC	28°26′S49°49′W
9	Pericó	SC	28°16′S49°49′W
9	São Joaquim	SC	28°15′S49°49′W
10	Urupema	SC	27°56′S49°49′W
11	Lages	SC	27°51′S50°36′W
12	Lebon Régis	SC	26°55′S50°50′W
12	Santa Cecília	SC	26°47′S50°50′W
13	Caçador	SC	26°46′S50°23′W
14	Matos Costa	SC	26°28′S51°51′W
15	Mafra	SC	26°08′S49°49′W
16	Parque Nacional do Iguaçu	PR	25°30′S53°48′W
17	Curitiba	PR	25°25′S49°15′W
18	Ilha do Cardoso	SP	25°08′S47°58′W
19	Bertioga	SP	23°51′S46°09′W
20	Jundiaí	SP	23°11′S46°52′W
21	Campinas	SP	22°59′S46°59′W
22	Maricá	RJ	22°55′S42°49′W
23	Camanducaia	MG	22°46′S46°08′W
23	Monte Verde	MG	22°52′S46°03′W
24	Piracicaba	SP	22°42′S47°34′W
25	Campos do Jordão	SP	22°41′S45°30′W
26	Engenheiro Passos	RJ	22°30′S44°41′W
26	Itatiaia	RJ	22°30′S44°34′W
26	Visconde de Mauá	RJ	22°19′S44°35′W
27	Passa Quatro	MG	22°23′S44°58′W
28	Mogi Guaçu	SP	22°15′S47°09′W
29	Poços de Caldas	MG	21°47′S46°34′W
30	Parque Estadual do Ibitipoca	MG	21°43′S43°54′W
31	Arceburgo	MG	21°22′S46°56′W
32	Ouro Branco	MG	20°30′S43°43′W
33	Formiga	MG	20°28′S45°26′W
34	Divinópolis	MG	20°08′S44°53′W
35	Caraça	MG	20°08′S43°30′W
36	Linhares	ES	19°25′S40°04′W
37	Serra do Cipó	MG	19°15′S43°43′W
38	Diamantina	MG	18°13′S43°43′W
39	Joaquim Felício	MG	17°43′S44°44′W
40	Grão Mogol	MG	16°34′S42°42′W

Appendix III

Full Scientific Names of Plants Cited in Appendix I

This appendix lists the full scientific names (including authority) of the species of host plants cited in the Appendix I.

Acritopappus longifolius (Gardner) R.M. King & H. Rob.
Adenostemma lavenia (L.) Kuntze
Ageratum conyzoides L.
Ageratum fastigiatum (Gardner) R.M. King and H. Rob.
Aspilia cylindrocephala H. Rob.
Aspilia foliacea Baker
Aspilia jolyana Barroso
Aspilia laevissima Baker
Aspilia pascalioides Griseb.
Austroeupatorium inulaefolium (Kunth) R.M. King & H. Rob.
Austroeupatorium paulinum (DC.) R.M. King & H. Rob.
Austroeupatorium picturatum (Malme) R.M. King & H. Rob.
Austroeupatorium silphiifolium (Mart.) R.M. King & H. Rob.
Ayapana amygdalina (Lam.) R.M. King & H. Rob.
Baccharis aphylla Sch. Bip.
Baccharis brachylaenoides var. ligustrina (DC.) Maguire & Wurdack
Baccharis dracunculifolia DC.
Baccharis helichrysoides DC.
Baccharis leucopappa DC.
Baccharis punctulata DC.
Baccharis ramosissima Gardner
Baccharis serrulata DC.
Baccharis trinervis Pers.
Baccharis uncinella DC.
Barrosoa betonicaeformis (DC.) R.M. King & H. Rob.
Bidens brasiliensis Sherff
Bidens pilosa L.
Calea elongata Baker
Calea graminifolia Sch.-Bip. ex Kraschen.
Calea nitida Less.
Calea oxyleps Baker
Campovassouria cruciata (Vell.) R.M. King & H. Rob.
Campuloclinium campuloclinoides (Baker) R.M. King & H. Rob.
Campuloclinium chlorolepis (Baker) R.M. King & H. Rob.
Campuloclinium macrocephalum (Less.) DC.
Campuloclinium megacephalum (Mart. ex Baker) R.M. King & H. Rob.
Campuloclinium purpurascens (Sch. Bip. ex Baker) R.M. King & H. Rob.
Centratherum punctatum Cass.
Chresta sphaerocephala DC.
Chromolaena ascendens (Sch. Bip. ex Baker) R.M. King & H. Rob.
Chromolaena barbacensis (Hieron.) R.M. King & H. Rob.
Chromolaena chaseae (B.L. Rob.) R.M. King & H. Rob.
Chromolaena congesta (Hook. & Arn.) R.M. King & H. Rob.
Chromolaena costatipes (B.L. Rob.) R.M. King & H. Rob.
Chromolaena cylindrocephala (Sch. Bip. ex Baker) R.M. King & H. Rob.
Chromolaena decumbens Gardner
Chromolaena hockeriana (Griseb.) R.M. King & H. Rob.
Chromolaena horminoides DC.
Chromolaena laevigata (Lam.) R.M. King & H. Rob.
Chromolaena matogrossensis (Hieron.) R.M. King & H. Rob.
Chromolaena maximilianii (Hieron.) R.M. King & H. Rob.
Chromolaena minasgeraesensis (Hieron.) R.M. King & H. Rob.
Chromolaena multiflosculosa (DC.) R.M. King & H. Rob.

APPENDIX III. Continued.

Chromolaena myriocephala (Gardner) R.M. King & H. Rob.
Chromolaena odorata (L.) R.M. King & H. Rob.
Chromolaena pedalis (Sch. Bip. ex Baker) R.M. King & H. Rob.
Chromolaena pungens (Gardner) R.M. King & H. Rob.
Chromolaena sagittifera (B.L. Rob.) R.M. King & H. Rob.
Chromolaena squalida (DC.) R.M. King & H. Rob.
Chromolaena stachyophylla (Spreng.) R.M. King & H. Rob.
Chrysolaena flexuosa (Sims) H. Rob.
Chrysolaena herbacea (Vell.) H. Rob.
Chrysolaena platensis (Spreng.) H. Rob.
Conyza bonariensis (L.) Cronquist
Conyza canadensis (L.) Cronquist
Cyrtocymura scorpioides (Lam.) H. Rob.
Echinochoryne schwenkiaefolia (Mart.) H. Rob.
Gochnatia amplexifolia (Gardner) Cabrera
Gochnatia barrosii Cabrera
Gochnatia floribunda Cabrera
Grazielia gaudichaudeana (DC.) R.M. King & H. Rob.
Grazielia intermedia (DC.) R.M. King & H. Rob.
Hatschbachiella tweedieana (Hook. & Arn.) R.M. King & H. Rob.
Heterocondylus alatus (Vell.) R.M. King & H. Rob.
Heterocondylus amphidictyus (DC.) R.M. King & H. Rob.
Heterocondylus grandis (Sch. Bip. ex Baker) R.M. King & H. Rob.
Heterocondylus jaraguensis (B.L. Rob.) R.M. King & H. Rob.
Heterothalamus psiadioides Less.
Inulopsis scaposa (Remy) Hoffm.
Jungia floribunda Less.
Koanophyllon adamantium (Gardner) R.M. King & H. Rob.
Koanophyllon thysanolepis (B.L. Rob) R.M. King & H. Rob.
Lepidaploa lilacina (Mart. ex DC.) H. Rob.
Lepidaploa salzmanii (DC.) H. Rob.
Lepidaploa spixiana (Mart. ex DC.) H. Rob.
Lessingianthus (Oligocephalus) desertorum (Mart. ex DC.) H. Rob.
Lessingianthus (Oligocephalus) simplex (Less.) H. Rob.
Lessingianthus (Oligocephalus) virgulatus (Mart. ex DC.) H. Rob.
Lessingianthus brevipetiolatus (Sch. Bip. ex Baker) H. Rob.
Lessingianthus buddleiifolius (Mart. ex DC.) H. Rob.
Lessingianthus carduoides (Baker) H. Rob.
Lessingianthus coriaceus (Less.) H. Rob.
Lessingianthus glabratus (Less.) H. Rob.
Lessingianthus hovaefolius (Gardn.) H. Rob.
Lessingianthus laevigatus (Mart. ex DC.) H. Rob.
Lessingianthus linearifolius (Less.) H. Rob.
Lessingianthus linearis (Spreng.) H. Rob.
Lessingianthus poliphyllus (Sch. Bip. ex Baker) H. Rob.
Lessingianthus psilophyllus (DC.) H. Rob.
Lessingianthus pumillus (Vell.) H. Rob.
Lessingianthus pycnostachyus (DC.) H. Rob.
Lessingianthus roseus (Mart. ex DC.) H. Rob.
Lessingianthus rosmarinifolius (Less.) H. Rob.
Lessingianthus rubricaulis (Humb. & Bonpl.) H. Rob.
Lessingianthus sellowii (Less.) H. Rob.
Lessingianthus stoechas (Mart. ex Baker) H. Rob.
Lessingianthus vepretorum (Mart. ex DC.) H. Rob.
Lessingianthus warmingianus (Baker) H. Rob.
Mikania cipoensis Barroso

Appendix III. Continued.

Mikania cordifolia (L. f.) Willd.
Mikania decumbens Malme
Mikania lasiandrae DC.
Mikansia micrantha H.B.K.
Mikania officinalis Mart.
Mikania purpurascens (Baker) R. King & H. Rob.
Mikania retifolia Sch. Bip. ex Baker
Mikania sessilifolia DC.
Moquinia racemosa (Spreng.) DC.
Pluchea laxiflora Hook. & Arn. ex Baker
Pluchea sagitalis (Lam.) Cabrera
Porophyllum riedelii Baker
Porophyllum ruderale (Jacq.) Cass.
Praxelis clematidea (Griseb.) R. King & H. Rob.
Proteopsis argentea Mart. & Zucc. ex Sch. Bip.
Pseudobrickellia brasiliensis (Spreng.) R. King & H. Rob.
Senecio brasiliensis (Spreng.) Less.
Senecio oxyphyllus DC.
Senecio selloi (Spreng.) DC.
Solidago chilensis Meyen
Stomathanthes polycephalus (Sch. Bip. ex Robinson) H. Rob.
Symphyopappus casarettoi B. Robinson
Symphyopappus cuneatus (DC.) Sch. Bip. ex Baker
Symphyopappus decussatus Turcz.
Symphyopappus itatiayensis (Hieron.) R. King & H. Rob.
Symphyopappus reticulatus Baker
Trichogonia hirtiflora (DC.) Sch. Bip. ex Baker
Trichogonia salviaefolia Gardner
Trichogonia villosa Sch. Bip. ex Baker
Trichogoniopsis adenantha (DC.) R. King & H. Rob.
Trixis mollissima D. Don
Trixis praestans (Vell.) Cabrera
Trixis vauthieri DC.
Trixis verbasciformis Less.
Verbesina subcordata DC.
Vernonanthura beyrichi (Less.) H. Rob.
Vernonanthura catharinensis (Cabrera) H. Rob.
Vernonanthura chamaedrys (Less.) H. Rob.
Vernonanthura glandulosa-dentata (Hieron.) H. Rob. in litt.
Vernonanthura mariana (Mart. ex Baker) H. Rob.
Vernonanthura membranacea (Gardn.) H. Rob.
Vernonanthura montevidensis (Spreng.) H. Rob.
Vernonanthura mucronulata (Less.) H. Rob.
Vernonanthura nudiflora (Less.) H. Rob.
Vernonanthura petiolaris (DC.) H. Rob.
Vernonanthura phaeoneura (Toledo) H. Rob.
Vernonanthura phosphorica (Vell.) H. Rob.
Vernonanthura subverticillata (Sch. Bip. ex Baker) H. Rob.
Vernonanthura tweedieana (Baker) H. Rob.
Vernonanthura westiniana (Less.) H. Rob.
Vernonia incana Less.
Vittetia orbiculata (DC.) R. King & H. Rob.
Wedelia paludosa DC.